

A CONSIDERATION OF VARIEGATION

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Received April 12, 1928

The segregation of albino or chlorophyll deficient seedlings in a pedigree propagated by self-fertilization is due either to a definite genetic factor or factors according to DEMEREC (1923) in maize, HALLQVIST (1926) in barley, etc., or to the abnormality of the plastids themselves according to CORRENS (1909) in *Mirabilis*, BAUR (1909) in *Pelargonium*, ANDERSON (1923) in maize, CLAUSEN (1927) in *Viola*, etc. In the former cases, the albino segregates occur in one-fourth, seven-sixteenths, one-sixteenth and so on, according to the number and behavior of the factors by which the deficiency of chlorophyll is manifested, while in the latter their segregating proportion is quite irregular, varying according to the degree of variegation on the parental plants from which the seeds were collected, or, in other words, the abnormal plastids conduct themselves independently of the genetic factors, their transmission therefore being non-Mendelian. Professor Sô (1921) studying the genetics of variegated barley made its peculiar behavior clear. His conclusions published in the Japanese language induced me to write this paper, in which I will give a critical discussion of the complicated heredity of some variegated plants in the light of Professor Sô's work and of analogous cases from observations made by myself.

I

Before entering into the main discussion, I will describe the results gained in my provisional studies on the variegated barley and rice. Once there came to my attention a case of the ordinary non-Mendelian variegation in barley. In 1923 I found a plant with coarse yellow stripes distributed over some leaves and an ear, and transplanted this to our experimental field to study its genetic nature. Owing to its poor growth and to transplantation at the flowering time, the seeds obtained were not numerous. From the green ears I raised 38 green seedlings, on which later no yellow stripes developed, and from the yellow part of a variegated ear 8 seedlings were obtained, all yellow, which died a few weeks after their germination.

Variegated seedlings are often found in rice, *Oryza sativa*, though they are rare in barley. In most cases the variegation occurs in coarse yellow stripes and is apt frequently to disappear in later growth. I collected the

seeds from a variegated rice plant and obtained 155 seedlings containing 48 yellows or 30.97 percent, the others being pure green, excepting one seedling which had a few yellow stripes on the lower leaf. The variegation on this specimen, however, completely disappeared in the later leaves and pure green ears only were produced. Although I did not carry out hybridization experiments with the green-and-yellow-variegated barley and rice, their non-Mendelian nature is certain from the abnormal segregation in their self-propagated progeny. The continuation of variegation of the ordinary non-Mendelian type by seeds is difficult in rice, and this is closely connected with its particularly coarse pattern of variegation. The cause of the variegated pattern, coarse or fine, of the non-Mendelian type was explained logically by WINGE (1919), who states in this connection: "Elementary mathematics will tell us that cells with a small number of green and white plastids will, by constant bisection in the course of a few cell generations, possibly even on the first division, give off both purely albinotic and self-colored green cells in the descendance, and only a very few of a mixed character, later none at all—whereas cells with but a slightly (not greatly) superior number of green and white plastids will only after a several cell generations, when the embryo has reached a considerable size, give off albinotic and self-colored green cells, and will never in the course of the ontogenesis lack cells with mixed contents" (p. 15). The different distribution of the abnormal plastids will give the corresponding difference in the proportion of variegateds in the offspring. Barley and rice stand at one extreme in regard to the small number of plastids contained in a cell, among the known non-Mendelian variegated plants. If this is the case the variegation should give a coarse pattern and the specimens should give a progeny containing green and yellow seedlings with a few or no variegateds, as actually recorded. On reading the subsequent sections we must bear in mind that the sorting out of the homogeneous plastids will occur very easily in barley and rice in the course of cell multiplication.

II

Among the specimens of barley cultivated in our College there is a variegated variety named "Okina" (old man). The foliage and ears of this variety are variegated with fine white stripes, and its varietal name came from its ears bearing some long white awns, reminding one of an old-man's white hair. The progeny of this variety contains some white seedlings, which die in a few weeks after germination when the food stored up in the endosperm is consumed. The proportion of albino

seedlings varies to some extent according to different samplings, though, on the whole, it is almost fixed. The seedlings, other than albinos, invariably grow up to be variegated. Observation on fully grown plants shows constancy in these respects. The variegated characteristic is segregated as a Mendelian recessive to the normal green. Sô (1921) studied thoroughly the genetic behavior of the variegation of this variety, and his main results, freely translated from the Japanese, are as follows:

1. The albinism is transmitted only maternally, the pollen having no immediate connection with it.
2. Variegation behaves as a recessive to green.
3. In F_2 and later generations, the segregation of variegation occurs in a monohybrid ratio.
4. In crossing experiments, the pollen of pure white glumes is not different in its effect from that of green ones of the variegated ear.

On the basis of these experimental facts he developed his theory to account for the special behavior of the variegated barley in inheritance. The variegated character is transmitted as a recessive genetic factor, but it is not a pattern factor in a strict sense, because the white parts or stripes are due to the distribution of white plastids which have changed their quality permanently. The variegation is, therefore, produced by a factor which alters at times the essential quality of the plastids from normal green to colorless. The original difference between green and variegated barley lies in their allelomorphs for the stability of the plastid, and the variegation is due to the development of white stripes, owing to the distribution of the white plastids controlled no longer by genetic factors. To be more particular, let us designate the allelomorphs concerning the plastid mutability by G (dominant) and G' (recessive). Normal green barley is GG , and the variegated barley $G'G'$. The plastids of both are originally quite normal in their essential quality. Each of them is designated by g . It is assumed that in the presence of $G'G'$ (double recessive) some of the green plastids mutate at times to white plastids (w). The plastids of self-green barley are all g , while those of the variegated barley consist of g and w . The former (g) may subsequently be altered in the presence of the factors $G'G'$ to become white.

The plastid mutation, that is sometimes observed in various plants, is due in almost all cases to sporadic events and does not seem to be a habitual phenomenon. In the "Okina"-barley, however, the plastid mutation repeats itself so frequently in the course of the development of the plant body that not a single individual or even a leaf or an ear,

which is free from the variability or self-green, is produced. The variegated segregates appear in a recessive proportion from green hybrid plants. According to Sö's experiments, the white plastids are transmitted maternally. Under such circumstances, the reciprocal crossings of the normal and variegated varieties give partly different results in F_1 , while practically the same in the later generations. Figure 1 is a diagrammatic

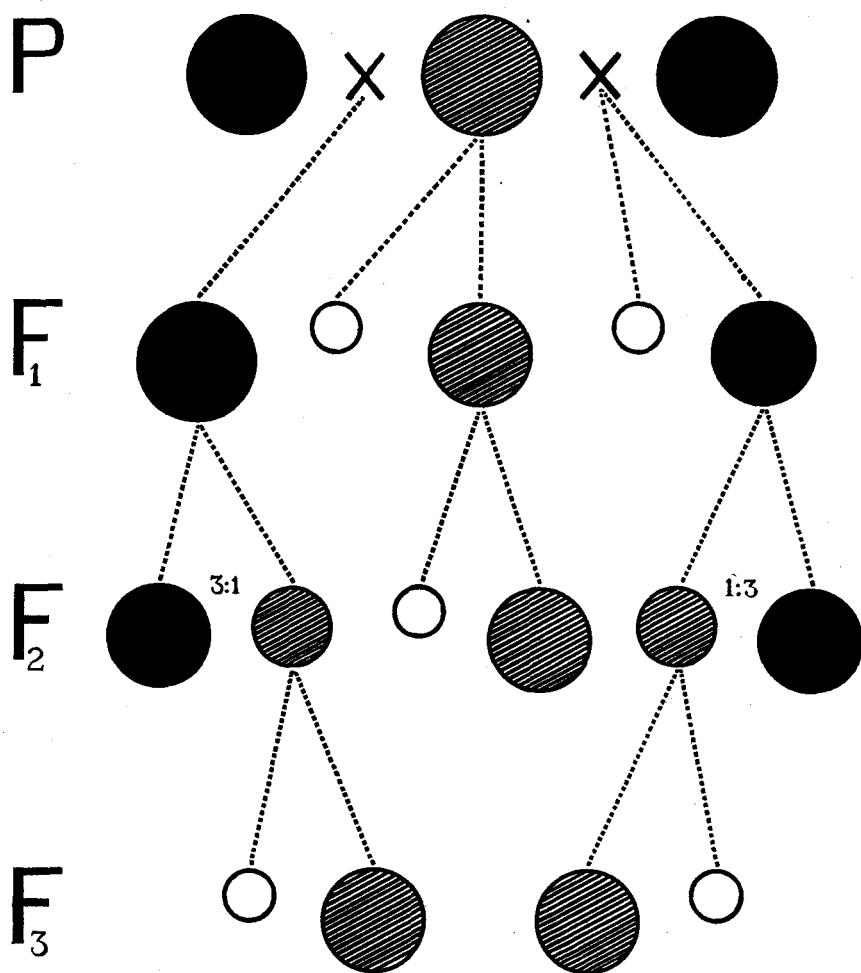


FIGURE 1.—Showing the heredity of variegated barley of the "special" type. The black circle indicates the green plants, the barred the variegated and the blank circle the albinotic. The size of the circles roughly represents the proportion of the respective segregates in a pedigree. The left group of F_1 , F_2 and F_3 shows the results of cross-breeding of green (φ) \times variegated (σ), those in the center the inbreeding of the variegated, and those at the right the cross-breeding of variegated (φ) \times green (σ).

summary of inbreeding and cross-breeding of the "Okina"-barley, drawn from the results obtained by Sô. In barley the chance that white plastids and green ones are present in an egg-cell of a variegated plant may not be frequent, because the sorting out of homogeneous plastids will occur very easily in the foregoing cell-division, and yet the seedlings other than albinos are finely variegated, due to new plastid mutations occurring in their later embryonic stage. Sometimes the variegation of the seedlings is not clear, but successive observation make its existence manifest. The absence of pure white leaves and ears on the field-grown variegated barley, according to my opinion, may be regarded as due to the non-mutability of plastids in cells of the primitive ontogenic stage, including the rudiments of leaves and ears. As a result of this, there is no chance of obtaining pure white leaves or ears developed from white cells forming their rudiments. The absence of plastid mutability seems also to be the case in gametogenesis as well as in later somatic divisions. The plastid mutation occurs repeatedly during the development of the somatic tissues, excepting its very earlier and later times, and by the sorting out of the albinotic plastids the white stripes appear on the foliage. But owing to the non-mutability in the later somatogenesis the purity of cells for their plastids will be maintained. As a natural sequence we should obtain almost exclusively two kinds of gametes, the one containing all green plastids and the other all whites, by the variegated plants, in the same way as those of the ordinary non-Mendelian type. The data obtained by the crossing variegated (φ) \times green (σ), which give rise to pure green and albino seedlings in F_1 , confirms this view. Practically, however, a few seedlings assuming a sectorial mosaic of white and variegated (or white and apparently green), though they rarely occur, are found among the progeny of variegated barley under my observation. According to my view, they must be regarded as developed from egg-cells containing green and white plastids together. If such seedlings are carefully cultivated we should obtain either white leaves or white ears, which are never found in the field-grown variegated barley in question, so far as our observation goes. Summing up, the plastid mutation period seems to begin at a late embryonic stage but ceases in later somatogenesis.

The variegation of the barley, therefore, is due to the distribution of a non-Mendelian albinotic character, but the causes of its repeated occurrence is due to a Mendelian factor. The genetics of this variegated barley is not comparable with the ordinary variegations studied in various plants, the case being "special" in its behavior. The variegation

in my yellow-striped barley was coarse, but that of "Okina"-barley is relatively fine; the difference is accounted for by the different genetic conditions by which the variegation appears.

III

Recently KONDÔ, TAKEDA and FUJOMOTO (1927)¹ have published a paper on the genetics of variegated rice from pedigree cultures of this plant. Their green-and-white-variegated races of rice are grouped under two classes in regard to hereditary type; in one the variegateds reappear in great numbers in the progeny, and in the other practically no variegateds are present but segregation produces green and white seedlings. The latter may be identified with that described in Section I. Among their experiments, A and B are treated principally as one and the same, therefore I will consider them together in the following discussion. In these experiments they obtained 64.5 percent of albino seedlings in the progenies of the variegated plants, the others being apparently green. When these green seedlings are transplanted into the paddy-field in order to allow their later growth, the majority grow up to be variegated and a few remain normal. The average proportion of white, variegated and green plants are 64.5 percent, 30.8 percent and 4.8 percent respectively. The albinos die soon after their germination. The green plants, which appear in the progeny of the variegated rice, breed invariably true to the type, while the variegated sisters repeat the occurrence of three forms in their offspring. With such an hereditary nature we cannot think of Mendelian segregation or ever-occurring factorial mutation. KONDÔ and his collaborators also made a hybridization experiment. They made a cross of variegated by green, from which they obtained variegated F_1 plants and bred an F_2 consisting 77.6 percent of albinos, 18.0 percent of variegateds and 4.4 percent of greens. This result is principally the same as that obtained by inbreeding the variegated rice in question. In the reciprocal crossing, they obtained only green F_1 plants. Therefore, the heredity of variegation in rice is maternal. The experiment C made by them gave quite a different result, though practically the same as in my case. My view of this is that it is due to ordinary non-Mendelian inheritance. KONDÔ and others regarded this and the former as equally ordinary non-Mendelian cases and their quantitative difference in the progeny was attributed to the occurrence of sterile flowers. The experiment C was made with variegated rice which was

¹ Their Japanese paper was published in the Journal of Scientific Agricultural Society, No. 277 pp. 443-462, 1925.

semi-sterile at the same time. The albinos obtained from four variegated plants were only 4.9 percent of their offspring, the others being pure green without exceptions. In their opinion this result is explained as follows:

“Vielleicht gibt es sehr viele Blüten, welche die Eigenschaften der Albino und zugleich die der Sterilität besitzen, was die Minderung der Prozentzahl der Albino bei Versuch C verursachen könnte” (loc. cit., p. 301).

The principal diversity of two variegated types of rice lies in the considerable difference of the frequency in appearance of variegated individuals in the succeeding generations. The genetic type of the variegation treated by KONDÔ and his collaborators in their experiments A and B does not seem to be thoroughly clear from the theory proposed by them. In my opinion, the case is complicated by the habitual occurrence of plastid mutation as shown in barley, therefore we meet with another not common case of non-Mendelian inheritance. The “unusual” type of variegation of rice has no connection with any factors contained in the chromosomes in its development as well as in its inheritance and the specimens carry quite normal genetic chlorophyll factors. The qualitative peculiarity of the cell-component of the variegateds in rice is due to the particular nature of the plastids themselves. The plastids may be normally green, containing ample chlorophyll, but it is their qualitative peculiarity that they are apt to alter themselves into white plastids. The habitual plastid mutability of this case is caused by the nature of the plastids themselves and this gives a contrast to the “special” form of the variegated barley due to the manifestation of a definite genetic factor, which stimulates the frequent occurrence of the plastid mutation. If we represent the abnormal green plastid by the symbol g' , an inconstant state, it at times transforms itself into w , which has an analogy to the white plastid of the “special” form of barley in its hereditary quality. As a result of the frequent occurrence of $g' \rightarrow w$, the white stripes will appear on the foliage and ears by the sorting out of cells, which contain only white plastids, and their multiplication in the course of plant development. These cells in turn produce albino seedlings in their offspring. The remarkable divergence in the proportions of albino seedlings between rice and barley, in which the respective average counts show about 65 percent and 7 percent, will roughly indicate the difference in the frequency of plastid mutation occurring in the mother plants. The absence of all white leaves and ears is quite comparable with that observed in the variegated barley of the “special” type. The frequency of the segregation of albino seedlings is rather fixed,

though it varies to some extent in different samplings, and this is owing to the fact that all ears are finely variegated, due to the frequent occurrence of plastid mutation. If the plastid mutation occurs also in the early ontogeny of an individual or the rudiment of an ear or a leaf and the frequency of alternation is very low or entirely absent, we should have no such rather fixed proportion in the segregation of albinos. The white stripes run longitudinally on leaves and stems extending to the ears; this tells the direction of cell division in the ontogeny of Gramineae; that is longitudinal divisions generally take place early, while the transverse divisions are on the whole late. Such a mode of organ formation will limit the extension of the breadth of white stripes, as in the cells forming rudiments of leaves and ears the plastid mutation does not generally occur, but naturally it helps to regulate the average proportion of the segregation of albino seedlings.

The appearance of green plants among the progeny of the variegated rice of the "unusual" form is, in my opinion, in accordance with the plastid mutation of $g' \rightarrow g$, the latter being the non-mutable state. The low proportion of the green offspring seems to be partly connected with the small distribution of green-glumed flowers in the panicle of the variegated rice, the fact suggesting a limited period at which the plastid mutation of $g' \rightarrow g$ occurs partly due to the low frequency of its mutability, though the occurrence appears to be habitual. Among the pedigrees of KONDÔ and others, the family E/1/2/3/4 contained 22.5 percent of green individuals; this seems to be due to the qualitative alteration of a plastid or plastids in relatively early plant growth.

According to KONDÔ and his collaborators the original "unusual" variegateds, with which they carried on their experiments above cited, made their appearance as seed variation. The existence of such plants among pure green pedigrees may on the other hand be attributed to simultaneous or successive alternation of the plastids contained in an egg-cell. Supposing that the plastids of one egg-cell are all transformed from g to g' , the cell could develop into a variegated plant after fertilization, since the pollen contributes no plastids to the egg in this species.

Before the publication of KONDÔ, TAKEDA and FUJIMOTO's paper, TAKEZAKI (1922) discussed the genetics of variegated rice, the transmission of which can be identified with the "unusual" form of the former investigators. Strictly speaking, TAKEZAKI's result was verified by them. TAKEZAKI interprets his case in the ordinary non-Mendelian mode of inheritance, but it is equally due to the peculiar nature of plastids contained in his variegated rice. As regards his experiments I will especially

cite the results obtained by crossings, which were made in both reciprocal ways and traced up to F_2 . The F_1 plants obtained by the cross, variegated (φ) \times green (σ), consisted mostly of variegateds, the rest, 20 percent, being albinos. At the seedling observation of F_2 TAKEZAKI found 42 percent albinos, the others apparently green, which later turned into variegated plants containing 7.15 percent of green sisters.

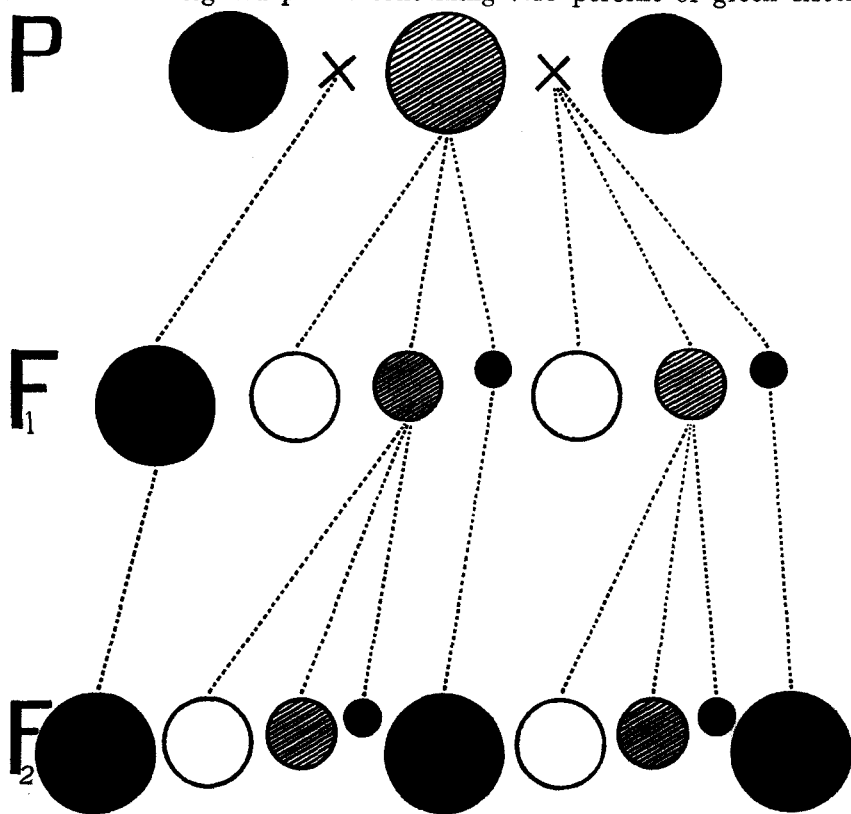


FIGURE 2.—This diagram as in figure 1 shows the hereditary mode of the variegated rice of the "unusual" type.

In the reciprocal crossing he obtained pure green F_1 and F_2 . With his experiments the evidence of the maternal inheritance is quite clear. The genetic nature of the "unusual"-typed variegated rice is shown graphically in figure 2, which is drawn in conformity with the theoretical explanation based on data obtained by TAKEZAKI, KONDÔ, etc.

IV

The non-Mendelian variegation is generally due to a mixture of abnormal plastids which have changed from the normal. The sporadic

plastid mutation occurs at times in various plants. In these cases, the green branches are often produced by the sorting out of green plastids in cell multiplication. If the plastid mutation is frequently repeated the green branches cannot remain as such owing to the successive occurrence of albinotic plastids, as demonstrated by barley and rice. I have called such cases "special" or "unusual" in contradistinction to the ordinary non-Mendelian variegation. There are several variegated plants which can be considered as analogous to the not-common class. The following garden varieties of coniferous plants came under my observation, and I have met with several similar cases in the other variegated plants, a discussion of which will be left for another opportunity.

Chamaecyparis obtusa, variegated.

The variegation occurs in creamy yellow color. The development of the yellow parts on the variegated plant is abnormal, resulting in greatly contracted branchlets.

Ch. obtusa var. *breviramea*, variegated (Jap. name "Shōnosuke-Hiba").

Greenish, creamy yellow variegation occurs on the foliage. Yellow branchlets of abnormal development are frequently produced. In this variety pure green branches are produced, which occurrence, however, cannot be comparable with that of yellow branches in frequency.

Ch. pisifera var. *breviramea*, variegated (Jap. name "Wakoku-Hiba").

This form has yellow patches on the foliage. The yellow parts have an arrested growth with relatively massive branchlets. Sometimes pure green branches appear on this variety.

Ch. pisifera var. *plumosa*, variegated.

White branchlets occur here and there on the plant. The variety seems to be rare in our gardens, so far as my observations go. I observed three individuals of this form, each growing about 1.5 metres high, but found no green branches. In another form, white branchlets occur in a pepper-and-salt pattern among the green foliage, with green sports appearing at intervals. The foliage of the latter variegated form, however, is somewhat contracted and has a delicate appearance, which distinguishes it from the former.

Ch. pisifera var. *filifera*, variegated.

The variegation occurs in yellow color. So far as my observation went, no green sports were found.

Juniperus chinensis, variegated.

A form with white variegation is found in the "Byakushin" type, in which needle-like foliage occurs abundantly. The other forms belonging to the "Ibuki" type, in which scale foliage occurs abundantly, are variegated with yellow or creamy white. The yellow or white branchlets are found very often in these varieties, probably in the most frequency among the variegated forms of the coniferous plants listed here. The green branches on these "Ibuki" forms are due to bud-sports, but not to the sorting out of the homogeneous green plastids, as is the case in the yellow or white branchlets. The green branches make usually very vigorous growth. In the yellow-

variegated form the yellow branchlets make somewhat strong growth in size compared with those of the white-variegated form, and the golden patches on the foliage is very evident by their frequent occurrences.

J. chinensis var. *procumbens*, variegated.

The variegation occurs in white, like that of the "Byakushin" type above listed, but the occurrence of white branches in the latter form is somewhat lower in frequency. In these two forms no green sports occur, so far as my observations go.

In these plants, the variegation is very evident, without any intergradation of color. The patch-work is generally maintained throughout the plant growth. Since the white or yellow patches occur in a coarse degree the vegetative segregation of abnormal plastids at cell multiplication must easily take place, resulting in yellow or white branchlets. If the variegation is due to the mixture of abnormal plastids and the plastid mutation is not repeated, the segregation of the green branches should be very frequent, though it never occurs by such a way in actual cases. Hence I consider them as analogous to the so-called "special" or "unusual" genetic form of variegation, in which albinotic plastids occur repeatedly by mutation.

As I did not raise the progeny of these variegated plants or hybridize them with their respective normal greens, I cannot draw a conclusion as to whether the cases are of the *Hordeum* or of the *Oryza* or of any other type. Some variegated plants shown in the list, however, sometimes bear green branches, which are considered to be produced by vegetative variation instead of segregation, as they are hardly comparable with white branches in frequency of their occurrence. The green branches make vigorous growth and become permanently green.

An interesting fact which came to my attention is the characteristic of the green reverting branches occurring on a white-variegated form of *Chamaecyparis pisifera* var. *plumosa*. The green sporting branches do not have a foliage habit quite similar to the variegated form, the foliage of which assume somewhat small and delicate appearance. This delicacy of the foliage may be due to the influence of genetic substances producing variegation. In the green sports, the genetic condition for chlorophyll production is recovered, and the branches, which live upon the delicate, variegated form, revert to the typical foliage of *Ch. pisifera* var. *plumosa*. Another variegated form of this variety, on which I failed to observe green sports, has, however, quite typical foliage. The dissimilarity in the type of foliage between these two variegated forms probably is caused by the difference of a genetic condition or genotype, by which the variegation is produced. Green sports make generally

vigorous growth compared with variegated, and they are wont to overcome the variegated stocks in growth. The undergrowth of the variegated branches is partly due to their genetic component by which the variegation is manifested, and partly to the frequent occurrence of the albinotic branchlets.

The color and growing habit of the albinotic branches on the variegated forms of the not-common type in various plants are not the same and sometimes very different, owing to the different nature of the factors or the unstable green plastids contained in the cells of the variegated forms at issue.

V

The habitual plastid mutability in the *Hordeum* type is due to the special quality of a definite factor and also due to a peculiarity of the plastid itself in the *Oryza* type. In both cases, the frequency of plastid mutability is affected by the influence of ontogenical stages of the plants. In barley the green hybrids carrying the GG' constitution give progenies containing green and variegated individuals at a 3:1 ratio, with no albinos. The dominance of the factor G , therefore, is complete. In addition to this, the plastid mutation does not seem to occur in gametogenesis or in the course of the primitive somatic development, and we have no chance of obtaining albino seedlings in the progeny of such heterozygous greens. The factor G' causes the frequent production of white plastids through the transformation of $g \rightarrow w$, and the factor itself is highly constant, so we have no green individuals among the progeny of the variegated barley in question. In rice, on the contrary, the green individuals appear almost habitually in the progeny of the variegated form of the "unusual" type. This is due to the change of the plastid itself from g' to g , but no factor concerns itself with this event. The frequent alternation of plastids occurs in two directions, $g' \rightarrow w$ and $g' \rightarrow g$, but these two differ in the frequency of occurrence and in the period at which the plastid mutation takes place. The difference in the latter suggests a delicate response of the plastids to the ontogenical environment of the plants in their transformation. The old stems of the variegated variety of *Juniperus chinensis* sometimes give buds which, however, are purely or almost white in the majority of cases, so far as my observation was made. The shooting branches of the variegated *Serissa foetida*, the quality of which is considered to be not common in its variegation, generally bear leaves with small white patches nearly green, while the lateral branches frequently are purely or almost white, especially with the plant

cultivated in a pot. The facts above cited show the delicate response of the plastids as to their transforming frequency in plant growth. KONDÔ, TAKEDA and FUJIMOTO's observation on mowed stocks of the variegated rice of the "unusual" type gives another confirmation of this relation. Their experiments revealed that "aus diesen Wurzelstocken trieben neue Pflanzen, und die Verfasser haben beobachtet, dasz aus den Wurzelstocken der gestreiften Pflanzen jedesmal in noch höherem Grade weissgestreifte . . . hervorkamen" (loc. cit. p. 312). The frequent occurrence of white or heavily variegated branches on the variegated plants of the "unusual" type may prove that simultaneous or successive plastid mutation takes place in the rudimentary cells of buds. This happening sustains my postulate as to the origin of the "unusual" type of rice with variegation, as tentatively suggested on a previous page.

Generally speaking, the segregation of albinos among a progeny propagated by the self-fertilization of heterozygous or variegated plants can be summed up as to their genetic types as follows:

- I. Mendelian case (figure 3-A).
- II. Non-Mendelian case.
 - 1. Ordinary form (figure 3-B).
 - 2. Not-ordinary form.
 - a. *Hordeum* type (figure 3-C)
 - b. *Oryza* type (figure 3-D)

In Mendelian segregation the albinism is due to an albino factor, which affecting the plastids make them outwardly colorless. The essential quality of albinotic plastids, however, is perfectly normal. Figure 3-A shows diagrammatically such a relation. The albinism of the ordinary form of non-Mendelian inheritance is due to the massive segregation of white plastids which character is manifested by their own abnormal quality and has no concern with any chlorophyll factors in their manifestation. Figure 3-B represents this relation and the origin of white and green segregates. The albinism of the "special"-typed barley is the same expression as that of the ordinary non-Mendelian case, due to the manifestation of the *w* plastids. But the cause of the successive occurrence of the white plastids is due to the factor *G'*, which at times alters the essential quality of plastids from *g* to *w*. Figure 3-C is drawn to demonstrate this relation. In the *Oryza* type the albinism is also due to the manifestation of the *w* plastids, the cause of the alteration, however, being attributable to the *g'* plastids themselves which may be phenotypically green, but lacking full constancy. The alteration of the plastids, therefore, occurs quite out of control of the genetic factors but

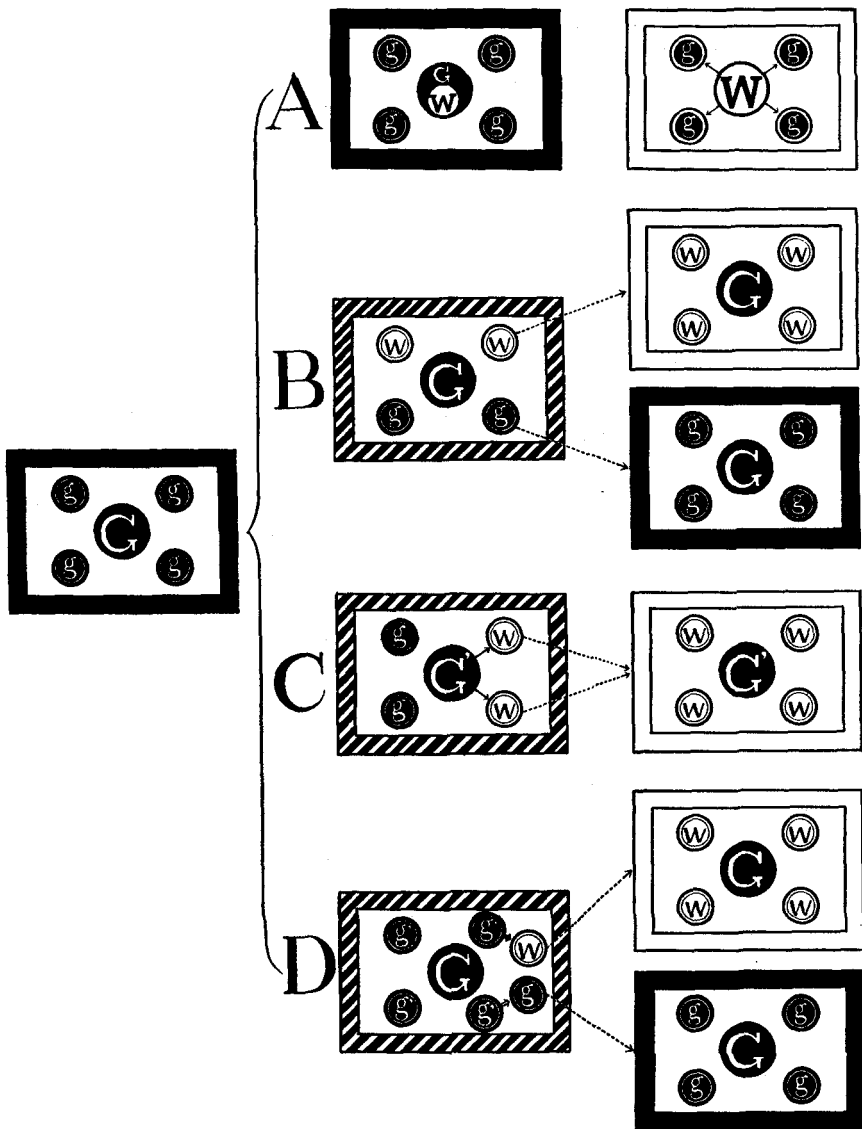


FIGURE 3.—A schema showing the genetic types of plastid inheritance, in which albino seedlings are segregated. A and B, Mendelian and ordinary non-Mendelian cases respectively; C, *Hordeum* type of the “special” form; and D, *Oryza* type of the “unusual” form. The left square shows the normal green condition. The squares in the center of the figure represent the variegated condition (heterozygote in A which is the Mendelian case). The squares to the right show the albinotic and the green plants sorted out from the respective central squares. Each square shows the model of a cell which contains one nucleus (the large central circle) and four plastids (small peripheral circles). The frame of the cell represents its color, the solid being that of a green cell; the barred that of a variegated cell; and the blank that of a white cell. The genotype of the cell is shown by the color and symbol given in its nucleus. The color of the rim of the plastid indicates its character, while the color and symbol of the center show its real quality.

directly from g' to w . The green individuals among the progeny of the variegated rice in question owe their origin to a similar process; namely, they originated by $g' \rightarrow g$. See figure 3-D, which shows these relations diagrammatically.

VI

The albinotic plastids with albino property usually have a fair constancy as to their quality, and the white cells propagate into purely white tissues or organs by their successive divisions. The common forms of the chlorophyll periclinals and reversals have purely white or yellow skins or cores, which character is non-Mendelian in inheritance, due to the constancy of the quality of the plastids contained in the cells. In some less-known chimaera plants, such as the periclinal variety of *Gardenia florida*, the white skin, which covers the green core, has green ticks and patches, the white tissues being never pure in color. CHITTENDEN (1925) published some interesting results gained in his experimental series of the chimaerical plants, *Hydrangea* and *Pelargonium*. The variegated forms, on which he made genetical and anatomical studies, contain some complicated chimaeras analogous to the variegated *Gardenia* above cited. In *Hydrangea*, he observed three variegated forms,² which, according to his denomination, are Types A,³ B and C, the latter

² The common white-over-green form is found in our *Hydrangeas*, but it was not present in CHITTENDEN'S collection.

³ To cite CHITTENDEN'S statement, this type "has the stems and the centres of the foliar organs solid white; the latter have a broad margin of solid green. This form, though frequently producing sports wholly green, shows otherwise great regularity of distribution in the type foliage" (loc. cit., p. 44). Such a sort of variegation or "peripheral" chimaera witnessed in some garden plants, is, according to my opinion, probably nothing but a periclinal, in which the yellow or white core seems to contain a toxin that affects the healthy plastids of some outer green tissue by assuming temporarily yellow or white color. The leaf margin of the variegated form, however, does not receive the influence of the toxin secreted by the core, and for that reason the leaf is marked with a green-and-yellow or green-and-white peripheral pattern. This view will explain quite satisfactorily the production of bud-sports, the behavior of which run remarkable parallel with the common periclinals. Among CHITTENDEN'S zonal *Pelargoniums*, *Freak of Nature* and *Happy Thought* seem to be modified periclinals of the green-over-white or green-over-yellow type, in which the white or yellow core affect the green skin at their outer surfaces on both sides of the leaves, resulting in peripheral chimaeras. Chittenden, however, seems not to agree on this view, as he states that "*Happy Thought* is evidently not a periclinal, for the central *aurea* tissue of the leaves is not covered by any other" (loc. cit., p. 51). This question will be solved by the assumption of a toxic substance, which affects the green plastids in dissolving their chlorophyll, secreted by the albinotic cells or plastids. If these chimaerical forms are Type A of *Hydrangea* and *Freak of Nature* and *Happy Thought* of *Pelargonium*, with which CHITTENDEN made breeding experiments, they should produce results like those expected from the breeding of the green-over-white or green-over-yellow periclinals. Actually CHITTENDEN'S description of the breeding aspect of the A-typed *Hydrangea* runs: "This green marginate Type A \times green (Type D) throws only

two of which will be treated in this text. Type B⁴ is a periclinal with green core which is covered by white skin containing green patches. According to him the breeding aspect of this form is as follows: "When a B Type is fertilized by a green Type D male, it gives both white and green seedlings; when, however, it is used as a male on a green Type D female, only green seedlings results" (loc. cit. p. 44). CHITTENDEN's Type C, however, is a periclinal with green core covered by white skin containing yellow patches instead of green ones.⁵ His breeding experiment gave the result that "When fertilized with pollen of a green (Type D), non-viable seedlings, some yellow and some white, result, whereas in the reciprocal cross, only green seedlings are produced" (p. 45). These and other results with *Hydrangea* led him to conclude that "... the seedlings, regardless of chlorophyll distribution in the male parent, reproduce only the types composing the actual leaf margin of the female." If so how can we understand the origin of green or yellow patches in white tissues? In my opinion, they are probably due to mutations of the albinotic plastids to the green ones, which distribute into massive cells after cell multiplication. The quality of the albinotic plastids contained in the white tissues of these periclinals is not manifested by nuclear substances, but due to the plastids themselves. The mutating green plastids may be induced by the alteration in the quality of the plastids. According to CHITTENDEN, *Freak of Nature*, whose stems, leaf-stalks and centres of leaves are white, produces white branches having minute green ticks at times on the margins of the stipules and rarely on the

green seedlings" (p. 44). By selfing the flowers of *Freak of Nature* he obtained eight seedlings, which were purely green. These results quite satisfy my view. *Happy Thought* gave segregating progeny in his examination, but, in my opinion, this was induced by the heterozygous genotype of the green skin of the variety. ROTH's experiments (1927) happened to prove the impure genotype of *Happy Thought*. So the conspicuous segregation does not contradict the periclinal view above proposed. The fact that the adventitious buds formed on the roots of *Freak of Nature* were always white in color will give an additional confirmation for the hypothesis, according to which the variety consists of periclinal mosaic tissues.

⁴ CHITTENDEN states: "This is a white-over-green periclinal, but differs from ordinary periclinal types in having lobes of solid green, without a white skin, irregularly distributed along the margin of the leaves. These lobes occur as outgrowths from the leaf margin. They project from the general contour of the leaf, and their growth is more ample than that of corresponding parts covered by the white skin. Sometimes such lobes are few, but generally several are borne by each leaf. The marginal lobes are usually separated by a white interval from the general body of the green core, and, though seeming occasionally to touch the inner green, they are separate developments, distinct from the core" (loc. cit., p. 44).

⁵ According to him, "This form is similar in chlorophyll distribution to Type B, but the lobes consist of pale yellow instead of green tissue. Here also the lobes are areas of rapid growth, and all degrees of lobing occur" (loc. cit., p. 44).

limbs of the leaves. His statement is—that “From such a branch, two wholly green seedlings were once raised; presumably they traced their origin to such a—potentially—green area” (p. 49). I regard the green ticks on the white branches to be due to their mutating origin. Golden Brilliantissima, one of periclinal Pelargoniums, whose behavior was examined by CHITTENDEN, is a form similar to Type B of his Hydrangea. From this form he obtained seven seedlings, all yellow in color, though white ones also may be expected to appear. The absence of white seedlings may possibly not be an incidental result, as he states: “Golden Brilliantissima sets seed badly; a large number of pollinations only produced 156 doubtful-looking seeds, of which 7 germinated” (p. 52). According to the experiment made by CLAUSEN (1927), the seeds of *Viola* containing white embryos, do not germinate. At present, however, we cannot draw any conclusion beyond a suggestive statement, and the solution of the problem can confirm a result of further experiments.

CONCLUSION

The inheritance of variegation of the ordinary non-Mendelian type in both barley and rice is closely connected with their particularly coarse pattern of variegation. It is suggested that variegation in these cases is due to sporadic mutation of the plastids themselves, which change from green to albinotic. When the abnormal plastids are later propagated and distributed in the tissues through cell multiplication variegated or albinotic bud-sports are produced. The factorial mutations are generally put into two categories of sporadic and habitual occurrences (IMAI 1927), and likewise the plastid mutations are not confined to sporadic occurrences.

Sô (1921) studied thoroughly the genetics of a finely variegated variety of barley and cleared up its special behavior. The variegated character is transmitted as a simple recessive to the green. The white stripes on the variegated foliage, however, are due to the distribution of white plastids, which have changed their own quality permanently by plastid mutation in the presence of certain recessive genetic factors. The plastid mutation in this case occurs quite habitually and it results in a fine pattern of variegation in this variety. The characteristic of the recessive factor which is contained in the cells of this variety, therefore, is that it alters at times the essential quality of some of the plastids from normal green to colorless. In this case, the plastid mutation occurs so frequently in the course of the development of the plant body that not a single individual or even a leaf or an ear, which is free from the variability or

self-green, is produced. This is interpreted to mean that the variegated character is transmitted itself as a simple Mendelian recessive to the green. The transmission of the white plastids, however, is maternal and does not follow Mendelian rules. So far as I can judge, the mutability of the plastid is not distributed over the whole cycle of the plant development, but the mutable period begins at a later embryonic stage and ceases in later somatogenesis. This assumption explains the particular points of this variegation. The genetics of this variegated barley, therefore, cannot be simply comparable with the ordinary variegation, the case being "special" in its behavior.

The variegated races of rice studied by KONDÔ, TAKEDA and FUJIMOTO (1927) are grouped under two classes in regard to their hereditary type: In one the variegateds reappear in a large proportion of the progeny, in the other practically no variegateds are present but segregation produces green and white seedlings. The latter is identified with the ordinary non-Mendelian case. In the former case, they obtained white, variegated and green progenies in the proportion of 64.5 percent, 30.8 percent and 4.8 percent respectively. The green plants breed invariably true to the type, whereas their variegated sisters repeat the previous performance. The variegation of rice is transmitted maternally in hybridization with green, and the variegated F_1 gives white, variegated and green F_2 segregates in roughly the same proportion as when the variegated plants are self-propagated. They, however, regarded all their cases equally as ordinary non-Mendelian inheritance. In my opinion, the present case is of a not-common form of non-Mendelian inheritance, that is, the plastid mutation occurs quite habitually like the variegated barley of the "special" type. The habitual plastid mutation is not due to any genetic factors contained in nucleus, but to the special quality of plastids themselves contained in the cells of this variegated rice. The plastids alter their quality from green to white by their own instability. The plastid mutation in this case, as in the variegated barley of the "special" type, seems to begin in the late embryonic stage and to cease in the late somatogenesis, including gametogenesis. The appearance of green plants among the progeny of the variegated rice of the "unusual" form is, in my opinion, in accordance with the plastid mutation of the unstable plastids to their non-mutable state. Before the appearance of KONDÔ and his collaborators' paper, TAKEZAKI (1922) published the similar data with variegated rice.

So far as I can judge, there are not a few variegated plants which may be classified under the not-common form in their genetic behavior, among which I have listed several coniferous plants. The plastid mutation

occurs habitually from green to colorless in these plants. Sometimes green branches, due to mutation, are produced on some of these variegated varieties.

The less-known periclinal chimaera plants which have green cores covered by white skins containing green patches, which CHITTENDEN (1925) studied, are interesting material for an investigation of plastid mutation. According to my view, the origination of green or yellow ticks in the white tissues of his chimaera plants may be due to the plastid mutation, occurring quite habitually, from white to green or to yellow.

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